

Phenotypic evidence for the specific and generic validity of *Heteroglaux blewitti*

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The genus *Heteroglaux* was established for the Forest Owlet *H. blewitti* when the species was first described, but owing to certain similarities with Spotted Owlet *Athene brama*, the use of *Heteroglaux* fell into disuse in the twentieth century until the species was rediscovered in 1997, and is still not universal; moreover, perceptions appear to linger that *blewitti* might even be conspecific with *brama* owing to a recent claim of interbreeding. In reality *blewitti* is distinct from *brama* on external morphology (plumage described elsewhere; narial position related to bill width; bill height; more heavily feathered toes; length of middle and hind claws; wing formula) and osteology, in which *blewitti* is distinct from all three species of *Athene* (multiple cranial elements, especially the greatly widened and inflated frontal, and the extremely stout tarsometatarsus). Lateral tail-flicking and direct, non-undulating flight further support generic separation.

INTRODUCTION

For well over a century the Forest Owlet *Heteroglaux* [*Athene*] *blewitti* remained as much a taxonomic as a conservation enigma. It was discovered in central India 140 years ago, and at once placed confidently in its own genus *Heteroglaux* by Hume (1873):

At first sight it would certainly be classed as an *Athene*; but the head is much smaller [*sic*: evidently a *lapsus* for 'larger'] than in any of the *Athene*'s I possess, *viz.*, *brama*, *radiata*, *malabarica*, *cuculoides*, *castaneonota*. The nostrils are not pierced from the front, backwards at the margin of a swollen cere, but are well inside the margin, and are pierced straight in. The upper surfaces of the toes, too, are not covered with bristles, but thickly feathered.

In the decade that followed, only six further specimens were taken (enumerated in Rasmussen & Collar 1998), and then the species disappeared. Perhaps as a consequence of this, its generic placement by Hume was never widely accepted. Although *Heteroglaux* continued to be used by Hume himself and some contemporaries (e.g. Hume 1879, Murray 1887, Sharpe 1891, 1899), from an early stage the Forest Owlet was also treated as congeneric with the Little Owl *Athene noctua* and Spotted Owlet *A. brama*, first in the genus *Carine*—even as early as Ball (1878), writing in Hume's own *Stray Feathers*—and more recently *Athene*. Although Gurney (1894) retained it in *Heteroglaux*, he cited Hume's (1873) view that it looks much like *A. brama* and added that Blanford considered it to belong to *Athene*; and the following year Blanford's (1895) treatment as such appeared. Dubois (1904) retained it in *Heteroglaux*, albeit without comment, but within a few decades virtually all works treated *blewitti* as an *Athene* (e.g. Baker 1934, Peters 1940, Biswas 1953, Ripley 1961, Abdulali 1972, Marshall & King 1988). Without explanation, Wolters (1975) assigned both *blewitti* and *brama* to the subgenus *Heteroglaux*, with *noctua* and Burrowing Owl *A. (Speotyto) cunicularia* occupying separate subgenera within *Athene*; otherwise *Heteroglaux* has only ever been used for *blewitti*. Voous (1989: 191) suggested that *blewitti* 'might provide a clue to understanding these relationships [between *Athene*, *Ninox* and *Glaucidium*], though the Forest Owlet may already be too close to the Spotted Owlet for that purpose'. Recent molecular phylogenies of owls (e.g. Wink *et al.* 2004, 2009) have not included *blewitti*.

Indeed, some considered the similarity of *brama* and *blewitti* so great as to render them conspecific. Baker (1923) treated *blewitti* as well as most subspecies of *brama*—all except, inexplicably

(perhaps as a *lapsus*), *A. brama tarayensis* of the north-western areas of the subcontinent—as races of *A. noctua*. This view, although not elsewhere accepted, may explain the listing in the NHMUK specimen register of the Davidson specimen (NHMUK 1925.12.23.958) that was stolen and remade by Richard Meinertzhagen (Rasmussen & Collar 1999) as '*Carine noctua blewitti*' [*sic*], although the other *blewitti* in the same accession (then NHMUK 1925.12.23.1, now MCZ 236630) was listed as *Athene blewitti*. The fictitious locality of the stolen specimen, which came to the (now) Natural History Museum, Tring, UK, in the late 1960s in Meinertzhagen's posthumous bequest (Rasmussen & Collar 1999), may in turn explain why it took until 1997 before the Forest Owlet was seen in the twentieth century (King & Rasmussen 1998). Over much of the intervening period, however, in the absence of clear diagnostic illustrations and texts, the species was speculated or judged to be so close in appearance to *A. brama* that it would be difficult and perhaps impossible to distinguish it (Ripley 1976, Ali 1978, Ali & Ripley 1981), and consequently the few reports or claims of *blewitti* that appeared in the interim were shown upon scrutiny to be *brama* (Rasmussen & Collar 1998).

Following the rediscovery of the species there has been a degree of conservation-oriented research focusing on its distribution and ecology (Jathar & Rahmani 2002, 2004, Rahmani & Jathar 2004, Ishtiaq & Rahmani 2005, Kasambe *et al.* 2005, Mehta *et al.* 2008, Chavan & Rithe 2009, Yosef *et al.* 2010). However, one aspect of its resurrection has remained unexplored: the issue of its generic identity. Publications at the time of the rediscovery and in its immediate aftermath mentioned both *Athene* and *Heteroglaux* in their titles (King & Rasmussen 1998, Rasmussen & Collar 1998, 1999, Rasmussen & Ishtiaq 1999). The two major monographic treatments of owls that appeared at this time (del Hoyo *et al.* 1999, König *et al.* 1999), both of which cited the preceding references, elected to retain the species in *Athene*, although the latter entered a caveat that its tail-flicking habit 'argues against a close relationship with other *Athene* owls and suggests closer affinity with pygmy owls (*Glaucidium*)', and consequently proposed 'placing this species in the subgenus *Heteroglaux*'.

In the twenty-first century the trend has clearly been towards accepting *Heteroglaux* as a valid monotypic genus. Collar *et al.* (2001: 1775) remarked that despite the species's 'strong superficial resemblance' to *Athene* 'its original placement in its own genus appears well justified based on osteological evidence (Rasmussen & Collar in prep.) and on recent behavioural observations including flight pattern and song (Rasmussen & Ishtiaq 1999)'. Thereafter, world lists (Dickinson 2003, Gill & Wright 2006), Indian avifaunas (Rasmussen & Anderton 2005,

Grimmett *et al.* 2011), one monograph (Mikkola 2012) and many journal papers and reports (preceding paragraph) have used *Heteroglaux*. Nevertheless, some sources have retained *Athene* (e.g. Clements 2007, König *et al.* 2008, Yosef *et al.* 2010), one even with the cryptic entry 'Remarks: Spurious use of the generic name *Heteroglaux*' (Weick 2006). This is perhaps unsurprising given that a clear case for the acceptance of this genus has never been made, and the osteological evidence referred to above never published. Here we seek to rectify these deficiencies.

This need is rendered all the more pressing following a recent report (Pande *et al.* 2011), albeit rejected (Ishtiaq 2011, Jathar & Patil 2011), of hybrid Forest Owlets \times Spotted Owlets. For this reason, we also consider the extensive structural differences between *blewitti* and *brama* beyond the plumage distinctions established in Rasmussen & Collar (1998). However, the exercise further requires the osteological analysis to extend beyond differences between these two species to cover not only all members of *Athene* but key representatives of other related owl genera (including *Surnia*, *Glaucidium*, *Xenoglaux*, *Micrathene*, *Athene*, *Aegolius* and *Ninox*: Ford 1967, del Hoyo *et al.* 1999).

METHODS

We considered two types of evidence: external morphology (focusing on the differences between *blewitti* and *brama*) and osteology (considering the differences between *blewitti* and *Athene*, thence to other genera). Plumage comparisons between *blewitti* and *brama* have previously been presented in Rasmussen & Collar (1998), and we therefore here restrict our comparisons of external morphology to mensural characters. We also briefly review data reported elsewhere for acoustics and behaviour.

External morphology of *blewitti* and *brama*

For the external morphological analysis we assembled for examination at the Natural History Museum, UK (NHMUK) all known specimens of *blewitti* (seven; four males, three females), and used the opportunity to compare them with other owl species, most importantly *Athene brama*, with which *blewitti* is ostensibly so closely allied as to have been considered conspecific (as noted above). We measured all specimens of *blewitti* (data in Rasmussen & Collar 1998) and specimens of *brama* at NHMUK; American Museum of Natural History, New York (AMNH); Academy of Natural Sciences of Philadelphia (ANSP); Museum of Comparative Zoology, Harvard University (MCZ); National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); and Zoological Survey of India, Calcutta (ZSI). This sample includes numerous representatives of each of the races of *brama* recognised by Peters (1940).

The specimens of *blewitti* were measured, x-rayed, photographed and videotaped in detail. Comparative measurements were also taken from 84 *brama* skins (37 males, 35 females, 12 unsexed) at AMNH (n = 19), ZSI (10), NHMUK (26) and USNM (29). Of the *brama* skins measured, 27 originated near known localities for *blewitti*, but specimens were included from throughout the range of *brama*. Measurements (in mm) taken from skin specimens were: culmen from base of skull; culmen from distal edge of cere; minimum width between nares; height of upper mandible at distal edge of cere; length of longest rectal bristle (straightened); tarsus; wing (straightened and flattened); tail (callipers inserted between central rectrices at insertion point); middle claw (digit 3) and hindclaw (digit 1, both claw measurements taken from the distal edge of scutes).

To compare wing formulae, shortfalls from the wing-tip of each of the primaries (P1–P10, numbered from the outside)

were measured (in mm) for six *blewitti* (one *blewitti*, NHMUK 1886.2.1.544, was excluded as its wing-tip is heavily worn) and 23 *brama* from USNM. The distances from the notches in the inner web to the tip of each of the outer four primaries (P1–P4) were also measured (in mm), as was the distance from the distal end (narrowest point) of the emargination on the outer webs to the feather tip for P2–P4. The notch for P4 was often not obvious in specimens of *brama*, and in these cases it was not measured.

Osteology

Measurements of skeletal features were taken directly from x-rays of *blewitti* and *brama* specimens, in which multiple views taken at various angles allowed direct comparisons with skeletal elements of *brama* and with the actual skin specimens x-rayed to ensure that the bones were oriented along the correct axes to avoid size distortion due to foreshortening. Only elements lying close to the film surface were measured to minimise parallax. Measurement options were limited by bone preservation and the fact that they are articulated in skin specimens of *blewitti*. Measurements taken were: greatest width of skull; lengths of humerus and ulna; length of carpometacarpus from proximal end to distal articular surface; length and minimum width of tibiotarsus, and width of its condylar end; and length and minimum width of tarsometatarsus.

Univariate statistics and principal components analysis (PCA) using correlation matrices were done separately on external, skeletal and wing formula measurements using SYSTAT for Windows (version 5). Variables used in PCA were chosen partially to maximise the number of specimens of *blewitti* that could be included without estimation of missing data. Because of the small sample of *blewitti*, sexes were combined.

Intergeneric skeletal comparisons

To allow osteological comparisons, several skeletal elements (the entire humerus, radius, ulna, tibiotarsus and tarsometatarsus; a femur missing the head; and the skull missing part of the posterior and caudal regions) were removed by J. P. Angle from the left side of a *blewitti* skin specimen (NHMUK 1886.2.1.546) using the techniques in Olson *et al.* (1987); casts were retained at USNM, as USNM 261299. These elements were compared directly with USNM skeletons of *A. brama* (n = 6); Little Owl *A. noctua* (10); Burrowing Owl *A. cunicularia* (5); Jungle Owllet *Glaucidium cuculoides* (7); White-browed Owl *Ninox supercilialis* (1); Brown Hawk Owl *N. scutulata* (3); Boreal Owl *Aegolius funereus* (1); and indirectly with *noctua* (4) and *brama* (2) from UMMZ. The UMMZ osteological specimens were examined the week following the USNM comparisons, and were videotaped to allow further study. In addition, important osteological features that were observed in the extracted *blewitti* skeletal elements were then examined (as possible) in the x-rays of all seven *blewitti* specimens and the x-rayed *brama*. Osteological terminology follows Howard (1929) and Baumel & Witmer (1993). Measurements taken of the above specimens, along with *brama* (9), *noctua* (4), *N. scutulata* (1) and Philippine Hawk Owl *N. philippensis centralis* (1) were: skull (including culmen) length; minimum widths of the frontal both anterior and posterior to the supraorbital processes; maximum skull width; height of lateral rim of frontal; width of distal half of lacrimal (maximum medio-lateral width); length of lacrimal (maximum antero-posterior length of caudal edge); maximum width across both palatines *in situ*; maximum length and minimum width of ulna; for humerus, femur, tibiotarsus and tarsometatarsus, maximum lengths, minimum widths and distal widths, and for the last two elements maximum proximal widths as well. For tibiotarsus, length was from the proximal articular surface, and proximal width did not include the fibula.

RESULTS

External morphology of *blewitti* and *brama*

The characters that separate *blewitti* from *brama* in the field are summarised in Rasmussen & Collar (1998). Even within a race, *brama* presents great variability in plumage and in most (but not all) of the characters distinguishing the two species a few individuals of *brama* closely approach the condition in *blewitti*, especially when the latter species is in worn plumage.

The nares are situated more widely apart in *blewitti* than in *brama*, owing largely to the broader culmen ridge of *blewitti* (Table 1). Moreover, the nares of *blewitti* are positioned more obliquely, not facing directly anteriorly as in *brama*. The cere of *blewitti* is less inflated and the nares are situated well inside the cere, instead of right at the edge of the more swollen cere, as in *brama*.

Compared to *brama*, *blewitti* has more heavily feathered toes (Hume 1873, Rasmussen & Collar 1998), except in the extremely worn specimen (NHMUK 1886.2.1.544). In most *blewitti* the white tarsal feathering continues uninterrupted onto the toes, while in *brama* the more mottled, dingier tarsal feathering stops more abruptly at the top of the toes, with only sparser bristles on the toes themselves. Although the extent of feathering on the tarsus and toes is often highly variable within an owl species (as it is in both Little and Burrowing Owls), the difference in this feature between the Forest and Spotted Owlets seems quite constant, allowing for the effects of wear. The toes and claws of *blewitti* appear noticeably heavier (and the latter longer; see below) than those of *brama*.

Although the four traditional external measurements (culmen, wing, tarsus and tail lengths) overlap broadly between *blewitti* and

Table 1. Summary statistics for measurements^a (mm) of *Heteroglaux blewitti* and *Athene brama* skin specimens (sexes combined) and results of Principal Components Analysis^b on these variables.

Measurements	<i>blewitti</i>				<i>brama</i>				Component loadings			
	Mean	SE	Range	N	Mean	SE	Range	N	PC1	PC2	PC3	
External measures												
Culmen from skull	21.2	0.8	19.9–22.0	7	20.5	1.1	17.4–23.7	83	0.31	–0.44	0.83	
Culmen from cere	14.7	0.6	13.7–15.8	7	13.7	0.7	11.9–15.8	81	–	–	–	
W between nares	5.4	0.4	5.0–6.0	7	3.4	0.4	2.6–4.3	63	0.87	0.07	0.02	
H upper mandible at cere	10.7	1.0	9.0–11.7	7	7.6	0.3	7.0–8.3	28	0.91	0.15	0.06	
Max. rectal bristle l	18.9	1.2	17.2–20.2	7	18.3	2.4	13.7–23.5	65	–	–	–	
Tarsus l	28.0	1.7	26.2–31.2	7	29.3	2.0	23.8–33.8	81	–0.40	–0.72	–0.26	
Wing l	147.8	3.2	144.0–154.0	7	153.2	5.8	139.0–169.0	80	–0.78	0.16	0.44	
Tail l	69.0	3.4	62.3–72.0	7	72.2	3.6	65.7–82.0	78	–0.69	0.55	0.17	
Middle claw (D3) l	14.1	0.8	13.1–15.2	7	10.6	0.6	9.5–12.1	62	0.92	0.67	0.03	
Hindclaw (D1) l	13.1	0.5	12.6–13.7	6	9.7	0.6	8.5–11.2	58	–	–	–	
Skeletal measurements from x-rays												
Skull w	36.2	1.49	33.8–37.5	5	33.3	1.25	31.4–34.8	16	–	–	–	
Humerus l	53.9	1.64	51.6–55.4	4	46.2	5.92	41.8–52.9	3	–	–	–	
Humerus distal w	9.5	0.34	9.0–9.8	4	8.5	0.39	7.7–8.9	9	–	–	–	
Ulna l	60.5	4.02	53.3–63.6	6	55.2	3.24	48.0–63.1	17	–	–	–	
Carpometacarpus l	38.6	1.64	27.2–31.4	7	26.6	1.22	23.6–28.2	21	0.73	0.52	–	
Tibiotarsus l	54.7	3.82	47.9–59.5	7	51.9	2.97	46.1–56.9	11	–	–	–	
Tibiotarsus w (min.)	3.5	0.35	3.1–3.9	7	2.9	0.16	2.7–3.3	17	0.91	–0.06	–	
External condyle w	8.0	0.68	7.5–9.3	7	6.8	0.61	5.4–8.1	17	0.88	0.22	–	
Tarsometatarsus l	26.8	1.47	24.7–28.2	7	28.9	1.55	25.7–31.8	20	–0.38	0.88	–	
Tarsometatarsus w (min.)	5.1	0.14	4.8–5.2	6	3.4	0.27	2.9–3.9	19	0.89	–0.20	–	
Wing formula measurements												
Shortfalls of each primary from wing point												
P1	26.7	2.7	23.0–30.1	6	25.5	3.0	19.6–29.5	23	–0.36	0.58	0.36	
P2	6.0	1.6	3.8–8.3	6	5.9	1.9	2.9–9.8	23	–0.34	0.80	0.07	
P3	0.3	0.6	0.0–1.5	6	0.3	0.6	0.0–2.1	23	0.02	0.04	0.82	
P4	0.2	0.3	0.0–0.5	6	0.5	0.8	0.0–2.5	23	0.34	–0.27	–0.58	
P5	3.4	0.7	2.7–4.6	6	4.6	1.7	1.0–7.9	23	0.67	–0.51	0.23	
P6	12.2	2.1	9.8–15.3	6	14.5	1.8	11.7–18.2	23	0.81	–0.47	0.08	
P7	19.3	2.3	16.7–22.2	6	24.3	2.8	20.1–30.7	24	0.87	–0.29	0.15	
P8	23.4	2.3	21.0–26.3	6	31.2	3.5	23.3–37.1	22	0.90	–0.13	0.21	
P9	27.8	3.2	24.0–33.5	6	36.2	3.4	29.7–42.0	22	0.92	–0.06	0.21	
P10	32.3	2.5	29.0–35.6	6	41.3	2.7	34.4–47.0	22	0.92	0.16	0.16	
Distance from notch to tip												
P1	32.3	4.2	28.0–39.7	6	39.1	3.0	31.0–45.8	23	0.82	0.08	–0.29	
P2	35.8	2.1	33.0–38.1	6	42.6	2.3	39.0–48.2	23	0.78	0.34	–0.17	
P3	33.3	1.9	30.9–36.0	6	39.4	2.2	35.4–43.4	23	0.78	0.42	–0.23	
P4	27.0	2.5	25.2–32.0	6	32.3	2.9	28.3–36.8	9	–	–	–	
Distance from emargination to tip												
P2	50.5	1.4	49.0–52.1	6	56.2	2.5	52.6–61.4	21	0.84	0.11	0.19	
P3	40.5	1.8	38.0–43.0	6	47.9	2.1	43.9–51.4	21	0.84	0.49	–0.10	
P4	31.8	1.6	30.0–34.0	6	39.1	1.6	35.5–41.5	21	0.81	0.52	–0.07	

^a l = length, w = width, h = height

^b Eigenvalues and percent variance explained for PC1–3 on external measures: 4.0, 44.3%; 1.6, 17.9%; 1.3, 14.3%, respectively; for PC1–2 on skeletal measures: 3.1, 61.6%; 1.1, 23.0%, respectively; for PC1–3 on wing formula measures: 8.7, 54.4%; 2.5, 15.6%; 1.6, 9.8%, respectively.

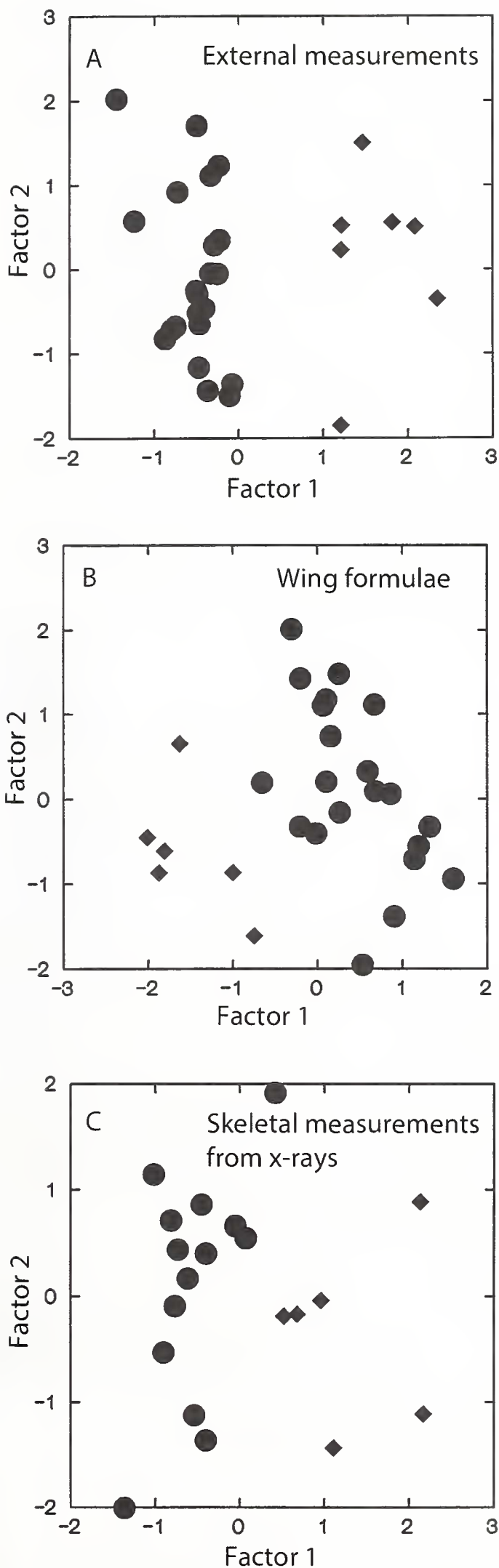


Figure 1. Graph of individual component scores on PC 1 and 2 for principal components analysis on measurements of *Heteroglaux blewitti* (diamonds) and *Athene brama* (circles). (A) external; (B) wing formula; (C) skeletal from x-rays.

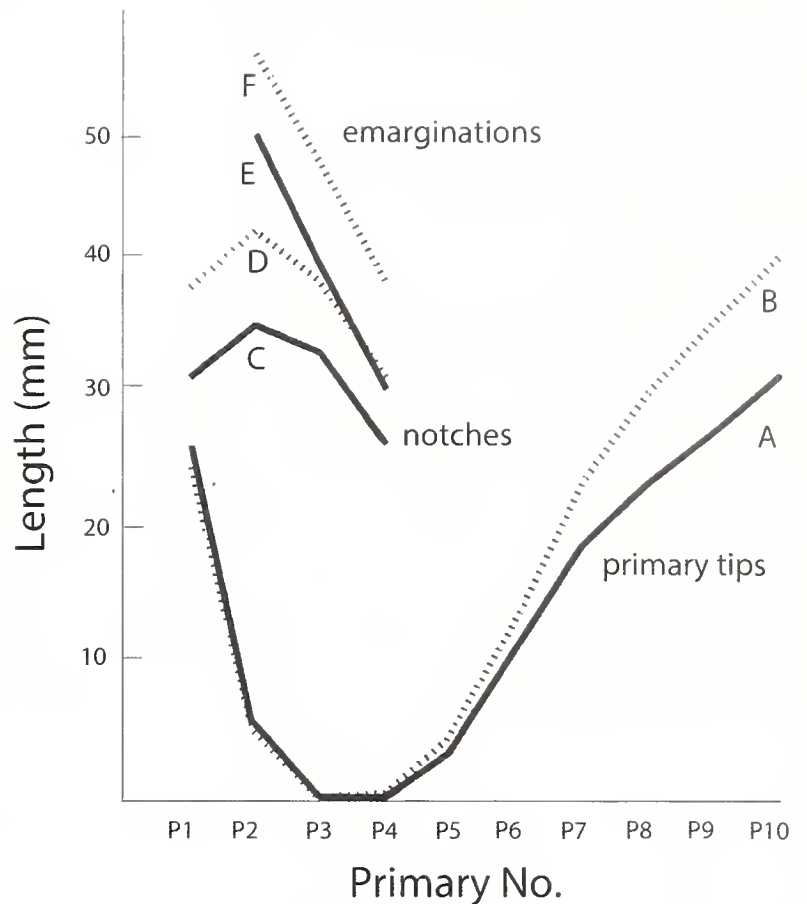


Figure 2. Wing formulae of *Heteroglaux blewitti* (solid lines, A,C,E) and *Athene brama* (dotted lines, B,D,F). (A,B) shortfalls from wing point of P1–10; distance from tips of individual feathers to (C,D) notches on inner webs of P1–4 and (E,F) emarginations on outer webs of P2–5 (descriptive statistics presented in Table 1).

brama, the taxa differ strongly in several other external mensural characters, even though sexes were combined owing to the small sample of *blewitti* (Table 1). External measurements that do not overlap between the two species are: width between nares, bill height and lengths of middle and hindclaws (Table 1). A PCA of external measurements (Table 1, Figure 1A) shows that by far the greatest proportion of the variance is explained on PC 1 by a contrast between middle claw length, width between nares, and upper mandible height *vs* tail and wing lengths. Complete separation between the species is attained on this axis (Figure 1A).

Several differences exist between the wing formulae of *blewitti* and *brama*, although most measurements overlap at least minimally between the species, and the sample of *blewitti* is small (Table 1, Figure 1B). In *blewitti*, P7–P10 each have a smaller shortfall, i.e. the feather tips fall closer to the wing-point, making the inner wing broader than in *brama* (Figure 2A,B). In *blewitti*, P7 is never as short as P1, while in *brama* P1 and P7 are approximately equal. The emarginations on the outer webs of P2–P4 and the notches on the inner webs of P1–P4 are all closer to the tips of the individual feathers in *blewitti* (Figure 2C–F); measurements of emargination position did not even overlap between the species (Table 1). Finally, 14 of 23 *brama* do not show a distinct notch on P4, whilst all six *blewitti* examined have a definite notch on the inner web of this primary.

A PCA of wing formulae showed that by far the greatest percentage of the variance was explained by Factor 1 (Table 1), which was mainly a size axis, on which shortfalls of P3 and P4 were not strongly correlated, and those of P1 and P2 were weakly negatively correlated. All *blewitti* had negative Factor 1 scores, while the scores of all *brama* fell above –1 on Factor 1, reflecting the smaller shortfalls of the inner primaries and notch and emargination distances of *blewitti* (Figure 1B).

Osteology

Despite the similarity in plumage of *blewitti* and *brama*, there are several major osteological differences (Plate 1) between *blewitti* and all three species normally recognised in *Athene* (including the highly polytypic *A. [Speotyto] cunicularia*).

Relative to *Athene*, the nasal process of the premaxillary of *blewitti* (Plate 1 A,B) is expanded anteriorly; the culmen ridge (Os nasale) of the premaxillary is more arched; the distal tip of the premaxillary is longer and more caudally directed, so the rostrum of *blewitti* is heavier and more strongly hooked; the narial openings are larger and more ovoid; the mandibular symphysis is broader; and the entire mandible is somewhat heavier.

The frontals of *blewitti* are much broader both anterior and posterior to the supraorbital process than for any *Athene* (Plate 1 A,B), so that the skull of *blewitti* strikingly resembles that of *Glaucidium* and *Ninox superciliaris*; the latter Malagasy species has been wrongly placed in *Ninox*, and is closer to *Athene*: H. F. James and S. L. Olson, pers. comm. 1997; Wink *et al.* 2004). The posterior portion of the interorbital roof of *blewitti* is not wider than the anterior portion, unlike *Athene*. The lateral rim of the frontal anterior to the supraorbital process is greatly inflated in *blewitti* compared to members of *Athene*, similar to but even more so than in *G. cuculoides*, *N. superciliaris* and most other small owls. The great inflation of this region is visible in x-rays of other *blewitti* specimens as well. The lacrimals of *blewitti* are very large relative to those of *Athene*, but like them (Ford 1967) are short and do not contact the jugal bar; those of the extracted skull of *blewitti* are detached from the skull, but their position relative to the jugal bar is confirmed by x-rays of all *blewitti* specimens. The maxillopalatines of *blewitti* are large, with straight medial edges that nearly contact each other for most of their length, unlike in *Athene*, where the maxillopalatines are more triangular in shape so that they only contact each other at the apex. The palatines of *blewitti* are relatively short anteroposteriorly as in *Athene* but are more expanded posteriorly, in the latter respect being similar to *G. cuculoides*. The supraorbital processes of *blewitti* are better developed than in most other *Athene* specimens we examined. The temporal fossa is much deeper in posterior view in *blewitti* than in *brama*.

The quadrate of *blewitti* has no intercapitular groove, the lack of which is apparently otherwise autapomorphic for *Athene* including *Speotyto* (Ford 1967); but the articular surface of the external capitulum is longer than in *Athene*, being similar to that of *G. cuculoides*. The otic process of the quadrate of *blewitti* is longer than in other owls examined, and the mandibular articulation is broad. The socket for the quadratojugal of *blewitti* is long and more strongly twisted externally than in *brama*, similar to that of *G. cuculoides*.

The humerus of *blewitti* is slightly longer and heavier than in *brama*, while the ulna of *blewitti*, although not longer, is substantially more robust. The leg proportions of *blewitti* (Table 2, Plate 1 C,D) are unusual in that the hindlimb is much more gracile proximally than distally: the femur and the proximal end of the tibiotarsus are heavier than those of *brama*, but not markedly so; however, the distal end of the tibiotarsus and the entire tarsometatarsus are greatly enlarged and especially broadened relative to those of *brama*. In addition, the single measurable femur of *blewitti* is longer than that of *brama*; the tibiotarsus is approximately the same length in both; and the tarsometatarsus of *blewitti* is shorter than that of *brama*, while the combined length of these three elements is roughly the same for the two species. The shaft widths of each of the leg elements in *brama* are very similar to one another, in strong contrast to the situation of *blewitti*, in which the tarsometatarsus shaft is much wider than that of the femur. In comparison to *blewitti*, *G. cuculoides* has all leg elements more uniformly stout: the femur and proximal tibiotarsus heavier, the tarsometatarsus similar in breadth but considerably longer. The

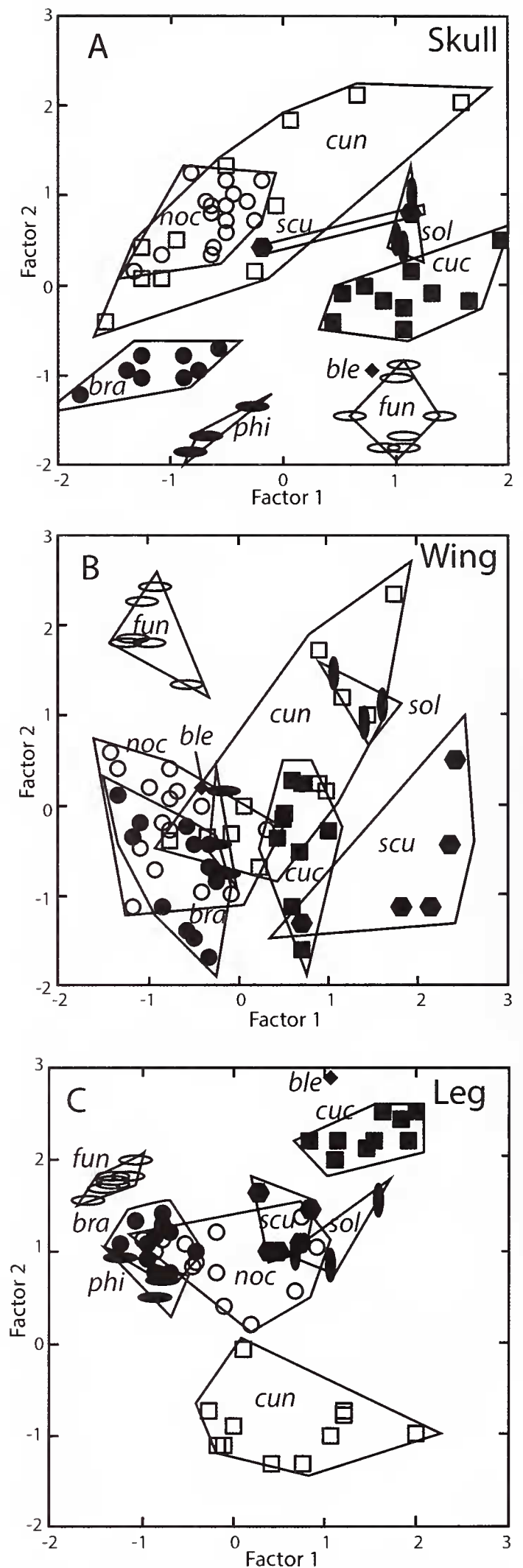


Figure 3. PCAs of skeletal measurements of selected surniine owls. *Athene noctua*, noc; *A. brama*, bra; *Heteroglaux blewitti*, ble; *A. cunicularia*, cun; *Ninox philippensis*, phi; *N. solomonis*, sol; *N. scutulata*, scu; *Aegolius funereus*, fun; and *Glaucidium cuculoides*, cuc. (A) skull; (B) forelimb; (C) hindlimb.

Table 2. Limb proportions of *Heteroglaux blewitti*, *Athene brama*, *Athene noctua*, *Glaucidium cuculoides*, and *Ninox superciliaris*. Ratios are of mean measurements.

Species	<i>blewitti</i> (n = 1)	<i>brama</i> (n = 6)	<i>noctua</i> (n = 10)	<i>cuculoides</i> (n = 7)	<i>superciliaris</i> (n = 1)
Wing proportions					
Hum l/distal w	5.76	5.64	5.64	5.37	
Hum l/ulna l	0.91	0.83	0.84	0.82	
Wing l ^a	107.8	104.5	106.3	119.0	
Leg proportions					
Femur l/distal w	4.88	5.23	5.12	4.78	
Tibiotarsus l/distal w	6.78	8.01	7.94	7.36	7.45
Tarsometatarsus l/distal w	2.95	4.33	4.53	3.32	3.71
Femur l/tib. l	0.74	0.67	0.68	0.71	
Tib. l/tar. l	1.98	1.71	1.66	1.96	1.91
Femur l/tarsometatarsus l	1.46	1.15	1.13	1.39	
Leg l ^b	115.6	115.7	123.5	125.8	
Wing l/leg l	0.93	0.90	0.86	0.95	

^aHumerus l + ulna l + carpometacarpus l

^bFemur l + tibiotarsus l + tarsometatarsus l

Plate 1. Comparisons between skeletal elements of *Heteroglaux blewitti* (NHMUK 1886.2.1.546) and *Athene brama* (NHMUK S/1989.25.4). (A,B) Skulls of (A) *blewitti* and (B) *brama* in cranial (top), lateral (middle), and caudal (bottom) views; (C,D) left femora, tibiotarsi, and tarsometatarsi of (C) *blewitti* and (D) *brama* in posterior view.

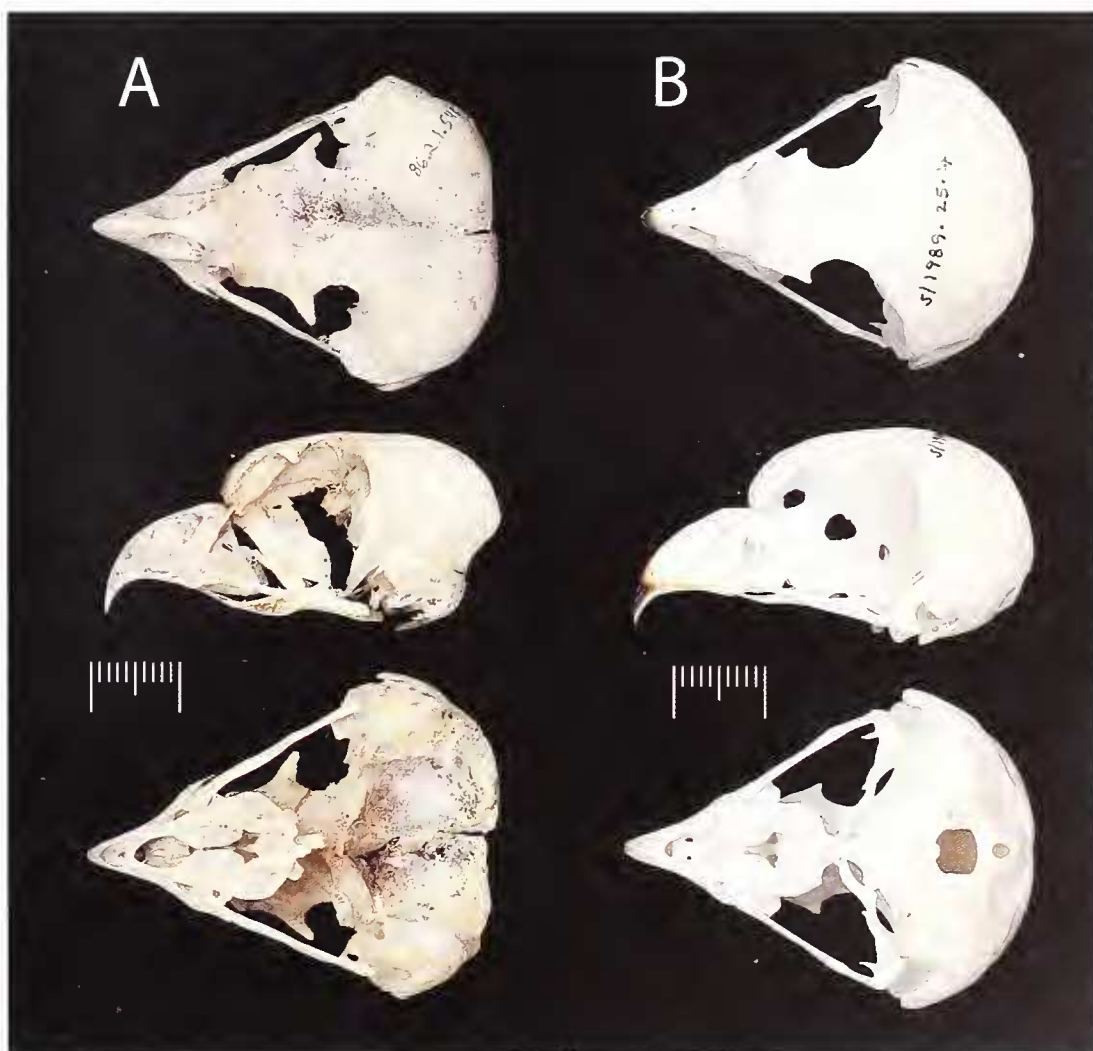


Table 3. Summary statistics of measurements^a (mm) and results of Principal Components Analysis^b on osteological measurements of selected owls.

Variable	<i>blewitti</i>	<i>brama</i>	<i>noctua</i>	<i>cunicularia</i>	<i>curculoides</i>	<i>fumereus</i>	<i>superiliaris</i>	<i>scutulata</i>	<i>philippensis</i> (s.l.)	<i>novaezeelandiae</i>	<i>solomonis</i>	Component loadings	
N	1	10–15	16	10–11	4–11	6–7	1	1–5	2–4	1	2–3	PCI	PCII
Skull													
Total l ^c	47.1±	46.1±1.3	48.0±0.9	49.0±3.2	50.6±0.8	47.8±0.5	52.5	51.4±5.5	46.4±0.3	47.8	51.3±0.5	0.73	0.53
		44.0–49.0	46.7–49.8	45.7–55.7	49.4–52.4	47.0–48.4		47.5–59.4	46.1–46.8		5.8–51.8		
Anterior frontal w	13.0	10.1±0.7	11.7±0.6	11.1±1.1	14.3±1.8	11.0±0.8	13.6	10.6±1.3	9.4±1.2	9.2	11.0±0.3	0.62	0.27
		8.9–11.4	10.6–12.9	9.2–13.1	11.7–17.0	9.5–12.0		12.3–14.4	13.2–15.1		10.8–13.3		
Posterior frontal w	13.0	10.1±0.9	8.5±0.8	8.5±1.2	15.8±1.2	15.7±0.6	14.6	13.5±1.0	14.4±0.9	11.7	12.0±1.2	0.79	-0.53
		8.9–12.1	7.3–9.8	7.1–11.1	13.7–17.5	14.7–16.5		12.3–14.4	13.2–15.1		10.8–13.3		
Maximum w	36.4	34.7±1.0	35.2±0.9	37.1±2.4	35.9±0.9	39.5±0.8	37.5	35.9±2.0	34.8±0.6	34.7	38.9±0.4	0.69	0.08
		33.2–35.9	33.1–36.8	34.5–41.6	33.7–37.0	38.6–40.6		34.0–39.0	34.4–35.5		38.4–39.1		
Lat. rim frontal ht	4.4	2.5±0.4	1.9±0.2	1.9±0.4	3.5±0.3	4.3±0.5	4.6	2.5±0.3	3.0±0.2	2.8	3.3±3.4	0.75	-0.61
		1.8–3.1	1.5–2.4	1.5–2.7	3.2–4.1	3.7–4.8		2.1–2.8	2.8–3.2		3.3–3.4		
Distal lacrimal w	4.4	2.5±0.5	2.6±0.3	2.7±0.6	2.5±0.3	3.2±0.4	2.7	2.5	2.6±0.3		2.9±0.2		
		2.1–3.8	1.8–3.0	1.8–4.1	2.2–3.0	2.7–3.8		2.4–2.8			2.8–3.1		
Lacrimal l	9.5	7.8±0.5	8.1±0.8	8.9±0.7	9.6±0.9	9.5±0.8	10.1	7.6	6.3±1.1		8.8±1.0		
		6.9–8.6	6.5–9.1	8.1–10.3	8.6–10.5	8.7–10.7			5.6–7.1		8.1–9.5		
Palatine w	11.8	10.1±0.8	11.5±0.6	11.3±0.7	11.8±0.6	11.9±0.3	12.9	12.7±0.3	10.7±0.2		12.8±0.4	0.72	0.38
		8.5–11.1	10.0–12.6	10.1–12.7	10.8–13.0	11.4–12.2		12.4–12.9	10.5–10.8		12.6–13.3		
Humerus													
Total l	51.3	47.4±1.2	48.5±1.7	55.9±4.0	53.7±1.4	47.6±0.5		60.9±3.0	52.3±1.1	55.3	59.9±0.9	0.96	0.12
		45.6–49.9	45.8–51.5	49.7–62.5	50.9–55.3	46.8–48.3		56.6–64.1	51.1–53.4		59.1–60.8		
Shaft w	3.4	3.5±0.2	3.4±0.2	3.6±0.2	3.8±0.2	3.2±0.1	4.1	4.4±0.3	3.5±0.6	4.0	4.2±0.1	0.93	-0.20
		3.1–3.8	3.0–3.7	3.3–3.9	3.6–4.2	3.0–3.4		3.9–4.7	3.5–3.6		4.1–4.3		
Distal w	8.9	8.4±0.3	8.6±0.5	9.2±0.6	10.0±0.4	8.4±0.1	10.4	11.0±0.8	9.3±0.2	10.1	10.7±0.4	0.94	0.01
		7.9–8.9	7.8–9.6	8.2–10.2	9.4–10.5	8.2–8.6		9.8–11.6	9.1–9.5		10.3–11.0		
Ulna													
Total l	56.5	57.1±1.6	57.8±2.0	70.0±4.9	65.3±1.9	54.4±1.0	68.0	70.7±4.4	60.1±2.1	63.4	68.4±1.3	0.92	0.06
		55.2–59.4	54.9–61.7	61.5–76.4	62.3–68.5	53.0–56.1		63.6–74.5	58.0–62.3		67.0–69.7		
Shaft w	2.6	2.5±0.2	2.5±0.2	2.7±0.2	2.8±0.1	2.3±0.2	3.1	3.0±0.1	2.4±0.2	2.6	2.6±0.1	0.81	-0.33
		2.2–2.9	2.1–3.0	2.4–3.0	2.6–3.0	2.2–2.7		2.9–3.1	2.3–2.7		2.5–2.7		
Femur													
Total l	38.1	34.5±0.6	36.9±1.5	39.1±2.6	40.2±1.0	36.3±0.7		38.5±0.8	34.6±1.3	37.6	40.8±1.4	0.88	-0.10
		33.1–35.4	35.0–39.6	35.8–44.2	38.3–42.4	35.1–37.3		37.3–39.5	33.1–35.6		39.6–42.4		
Shaft w	3.5	2.9±0.1	3.1±0.3	3.3±0.2	3.6±0.2	2.7±0.1		3.30.1	2.8±0.1	3.1	3.6±0.2	0.94	0.03
		2.7–3.1	2.7–3.7	2.9–3.6	3.3–3.9	2.5–2.9		3.2–3.5	2.7–2.9		3.4–3.8		
Distal w	7.8	6.6±0.2	7.2±0.4	7.2±0.4	8.4±0.4	6.2±0.1		8.0±0.3	6.9±0.2	7.3	8.2±0.3	0.96	0.03
		6.4–7.1	6.5–8.0	6.5–8.0	7.8–9.0	6.0–6.4		7.6–8.4	5.5–5.8		7.9–8.5		
Tibiotarsus													
Total l	51.5	51.3±1.6	54.0±2.7	67.7±3.0	56.7±1.3	48.0±0.5	59.6	60.2±2.2	55.7±1.8	59.3	61.4±1.7	0.64	-0.73
		48.7–54.3	50.2–59.2	62.9–73.5	55.2–58.8	47.4–49.0		57.3–63.3	53.5–57.8		60.3–63.4		
Prox. w	6.4	5.3±0.4	5.8±0.3	6.1±0.6	6.8±0.4	5.2±0.1	6.1	6.5±0.3	5.6±0.2	5.9	6.9±0.3	0.90	0.08
		4.7–5.9	5.3–6.2	5.4–7.0	6.2–7.7	5.1–5.4		6.2–6.9	5.5–5.8		6.6–7.1		
Shaft w	3.4	2.7±0.2	2.9±0.3	3.2±0.5	3.5±0.1	2.5±0.1	3.0	3.2±0.2	2.7±0.1	3.1	3.2±0.4	0.89	0.03
		2.4–3.1	2.6–3.5	3.0–3.5	3.3–3.7	2.4–2.8		3.1–3.5	2.6–2.8		2.9–3.6		
Distal w	7.6	6.4±0.2	6.8±0.4	7.1±0.5	7.7±0.3	5.9±0.2	8.0	6.7±0.33	6.1±0.3	3.4	7.5±0.4	0.93	0.01
		6.1–6.7	6.2–7.5	6.5–8.1	7.3–8.2	5.7–6.2		6.4–7.1	5.8–6.6		7.1–8.0		
Tarsometatarsus													
Total l	26.0	29.9±1.1	32.6±2.7	47.7±3.1	28.9±0.8	22.1±0.3	31.2	28.6±2.5	30.9±1.7	31.6	31.0±1.0	0.34	-0.90
		28.5–31.7	28.9–38.0	41.5–53.1	28.0–30.7	21.8–22.6		25.3–32.3	29.1–33.0		30.1–32.1		
Prox. w	7.8	6.7±0.2	7.0±0.6	7.3±0.6	8.2±0.4	6.1±0.1	7.5	7.3±0.4	6.3±0.5	7.0	7.8±0.3	0.93	0.09
		6.4–7.1	6.2–8.1	6.5–8.5	7.7–8.7	5.9–6.3		7.0–7.9	5.6–6.6		7.6–8.1		
Shaft w	5.3	3.2±0.1	3.3±0.3	2.9±0.4	5.0±0.2	3.4±0.2	4.3	3.8±0.2	3.0±0.1	3.4	4.0±0.3	0.65	0.72
		2.9–3.4	2.9–3.9	2.5–3.6	4.8–5.2	3.0–3.7		3.5–4.0	3.0–3.1		3.7–4.3		
Distal w	8.8	6.9±0.2	7.2±0.4	7.6±0.7	8.7±0.6	6.5±0.1	8.4	7.9±0.3	6.8±0.1	7.3	7.9±0.4	0.92	0.19
		6.5–7.1	6.6–8.0	6.9–8.9	7.2–9.3	6.2–6.6		7.6–8.4	6.7–6.9		7.6–8.3		

^a l = length, w = width, d = depth, ht = height, lat = lateral, prox = proximal^b eigenvalues and percent variance explained for PC1–2 on skull measures: 3.1, 51.5%; 1.1, 19.2%, respectively; on wing and skull length: 4.2, 70.8%; 1.0, 17.3%, respectively; on leg measures: 7.7, 70.1%; 1.9, 17.4%, respectively.^c also included in PCA of wing measures; component loadings on PC 1, 0.29; on PC 2, 0.93.

tibiotarsus and tarsometatarsus of *N. superciliaris* are much longer and more gracile than for any of the above species. The only osteological feature of the limbs listed by Ford (1967) as diagnostic of *Athene* (including *Speotyto*) is the pointed posterior edge of the outer rim of the middle trochlea of the tarsometatarsus; however, unlike *Athene* and like other owls examined, this is rounded in the single *blewitti* specimen.

Skull widths, length of wing elements (humerus, ulna and carpometacarpus) and widths of leg elements (tibiotarsus and tarsometatarsus) are all considerably larger in *blewitti* than in *brama* (Tables 1 and 3, Figure 1C). The tarsometatarsi of *blewitti* are no longer (averaging shorter) than in *brama*, but are considerably more robust (Tables 1 and 2). In a PCA of skeletal measurements (Table 1, Figure 1C), Factor 1 is a strong size axis on which tarsometatarsus length is negatively correlated; all *blewitti* scores fall above 0 on Factor 1, while most *brama* scores fall below 0.

Intergeneric skeletal comparisons

In PCAs of skull and hindlimb measures (Table 3, Figure 3A–C), scores for the single available *blewitti* skeleton fall well apart from those of any *Athene* species. On skull measurements (Table 3), *blewitti* is closest to *Aegolius funereus* and *Glaucidium cuculoides*, both of which have relatively large measurements on the variables included in the analysis (particularly so for width of frontal posterior to supraorbital process and height of lateral rim of frontal), and all have Factor 1 scores well above 0. *Athene* species, conversely, have small measurements on these variables, and all but a few large *cunicularia* fall below 0 on Factor 1. Factor 2 principally contrasts skull length with posterior frontal width and lateral rim height, and on this axis *blewitti* and *A. funereus* differ strongly from large *cunicularia*.

Wing proportions of *Athene* species and *blewitti* are very similar (Table 2, Figure 3B), with scores of all but large *cunicularia* falling below 0 on Factor 1, a strong size axis on which skull width is uncorrelated, indicating that, compared to other genera sampled, most *Athene* and *blewitti* have small wings relative to head size.

On a PCA of hindlimb measures (Table 3, Figure 3C), Factor 1 is a general size axis on which tarsometatarsus explains most variance, and on this axis *cunicularia* is the most distinctive group due to its extremely long legs, while *blewitti* is well separated from *Athene* and close to *G. cuculoides*. Factor 2 is basically a contrast between tibiotarsus and tarsometatarsus length with tarsometatarsus width, and on this axis *blewitti* has the highest score, again reflecting the stoutness of this element (see Table 2).

DISCUSSION

The specific validity of *blewitti*

There ought to be no question about the status of *blewitti* as a full species, but in the light of a recent report of a pair composed of a male *brama* and a female *blewitti* producing a supposedly fertile offspring, and indeed of a population of hybrids which ‘may have a much wider distribution that could equal or surpass the very limited one of the Forest Owllet’ (Pande *et al.* 2011), all of which could be taken to imply the conspecificity of the taxa, we briefly here recapitulate and expand the evidence.

First, *blewitti* differs in plumage and external structure from *brama* on multiple characters, including the narial and cere characters given in the species description by Hume (1873), and others enumerated in Rasmussen & Collar (1998); our elaboration above of the external structural differences involves much greater width between nares, bill height and claw length, plus a somewhat different wing-shape. It is interesting to note how, albeit with tiny sample sizes, the seemingly small size advantage of *blewitti* over *brama* translates into a doubling of body mass (241.0 g, n = 1 [based

on ‘8.5 oz’ on label of type specimen and in Hume 1873] vs 110–114 g, n = 2) (Dunning 1993). Second, *blewitti* possesses a wide range of osteological distinctions from not only *brama* but all members of *Athene*, including *cunicularia*. These involve many cranial characters (some on fused elements) on the nares, premaxillary, frontal, mandible, lacrimal, maxillopalatine and quadrate. Of these, the much broader frontal (on cranial view) with its greatly inflated lateral rim anteriorly is most striking. There are also differences between *blewitti* and *Athene* in hindlimb proportions, especially the short, very stout tarsometatarsus of *blewitti*, and in the conformation of the middle trochlea of the tarsometatarsus. Third, the song of *blewitti* is very dissimilar to vocalisations of *brama*, and does not support its treatment as a close relative (Rasmussen & Ishtiaq 1999, Jathar & Rahmani 2002, Rasmussen & Anderton 2005). Fourth, behavioural differences include the direct flight and lateral tail-flicking habits of *blewitti* (King & Rasmussen 1998, König *et al.* 1999, Rasmussen & Ishtiaq 1999, Pande *et al.* 2011, Mikkola 2012).

Finally, even if these many differences between the taxa are somehow not considered sufficient justification for the specific distinctness of *blewitti* from *brama*, the two forms are broadly sympatric: *brama* occurs wherever *blewitti* occurs. While the microhabitat where he collected them probably differed, J. Davidson collected at least 11 *brama* (all now in NHMUK) in the same region where he took his five *blewitti* (and other unattributed Khandesh and ‘Candesh’ specimens in the Hume and Seebohm collections may have also been collected by Davidson). Although Davidson took numerous egg sets of *brama* (Davidson MS) he never found a nest of *blewitti* (Barnes 1888), unsurprisingly since even in Khandesh in the 1880s the Spotted Owllet was clearly much the commoner species.

Sympatric occurrence is, of course, a prerequisite of hybridisation, but the evidence presented in Pande *et al.* (2011) is impossible to interpret owing to shortcomings in figure labelling, description and photograph quality. In our experience no specimens of *blewitti* or *brama* can be said to be intermediate in more than a few characters, and we have seen no specimens of either for which there is any doubt as to their specific identity. Based on the data presented above on plumage, other external morphological, mensural, mass and osteological differences, and the lack of intermediates, it is evident that *blewitti* is a well-marked, distinct species. Its coexistence with *brama* in areas where both are resident strongly reinforces this view. Thus, under any widely accepted species concept, the Forest Owllet must be considered specifically distinct from the Spotted Owllet. Until far better evidence is produced we take the view that hybridisation is unproven and, given the wide range of differences between the taxa, very unlikely. Even if occasional hybridisation were proven, wild intrageneric hybrids are known for several avian taxa (see McCarthy 2006), and these are not generally taken as evidence of exceptionally close relationship.

Baker’s (1923) notion of the conspecificity of *blewitti* with *noctua* has never been taken seriously elsewhere, but has never been explicitly dealt with; hence, we do so here. Although *A. noctua* is a variable species, it is considerably more different in appearance from *blewitti* than is *brama*. This is most evident in: the pattern of the underparts (streaked in *noctua*, barred in *blewitti*); crown pattern (streaked in *noctua*, nearly unmarked in *blewitti*); broader, spotted frontal semi-collar; less white on face; less banded wings and tail; smaller bill and claws; and tarsal length and shape (long and much more gracile in *noctua*, short and stout in *blewitti*). We can find no features in which *blewitti* resembles *noctua* more than it does *brama*, except for the streaked underparts of juvenile *blewitti* (Rasmussen & Anderton 2005). In osteology, *brama*, *noctua* and, except for tarsometatarsus length, *cunicularia* are very similar to each other, far more so than any is to *blewitti*.

The generic validity of *Heteroglaux*

Clearly the plumage differences between *blewitti* and established members of *Athene* are insufficient alone to justify the maintenance of *Heteroglaux*. Moreover, while the song of *blewitti* is very different from *brama* in its high pitch, tone and modulation, it does resemble the male song of *noctua* in overall quality; and even the song of *cunicularia* is somewhat intermediate between *blewitti* and *brama*. As a consequence we abandon the pursuit of generic limits in *blewitti* through acoustic evidence: such a line of taxonomic inquiry is untried elsewhere for fairly obvious reasons of interpretation (especially as convergence may play a part), and would require the discovery of very strong differences to be considered in any way informative. However, we note that while some vocalisations have been documented for *blewitti* (Rasmussen & Ishtiaq 1999, Ishtiaq & Rahmani 2005), to our knowledge only one recording is available online (AV 16764; <http://avocet.zoology.msu.edu/recordings/16764>), so detailed further analysis of vocalisations of *blewitti* cannot in any case be made until a more complete sample of recordings becomes available.

This then leaves morphological and behavioural differences to consider. In terms of external morphology, *blewitti* would not appear out of place within *Athene*. However, many osteological differences involving multiple cranial elements (especially the greatly widened and inflated frontal and the large, straight-edged maxillopalatines) and the hindlimb (the extremely stout tarsometatarsus) separate it from other *Athene*, and indicate that plumage convergence or perhaps even mimicry may have resulted in the relative similarity of external phenotype between *blewitti* and *brama*. It is unusual to find many marked qualitative (as opposed to mensural or quantitative) osteological differences within an avian genus, and it is even occasionally difficult to distinguish closely related genera osteologically.

Extinct island owls placed in *Athene* show great variation in size and length of extremities: one (*A. cretensis* of Crete) was relatively large, with very long tarsometatarsi (Weesie 1982), while another (*A. angelis* of Corsica) had unusually long femora and robust tarsometatarsi (Mourer-Chauviré *et al.* 1997), and a third (*A. vallgornerensis* of Mallorca) was small, with short, robust tarsometatarsi (Guerra *et al.* 2012). However, judging from figures (Guerra *et al.* 2012), even *A. vallgornerensis* had a distinctly less robust tarsometatarsus than does *blewitti*. Living and fossil island owls show no trend in overall size, but do tend to have somewhat larger feet and claws than closely allied continental species (Louchart 2005), as does the mainland *blewitti* to a striking degree.

Behaviourally, *blewitti* differs from other members of *Athene* in its direct, non-undulating flight, and in its lateral tail-flicking. While these differences by themselves may not suggest distinctness at the generic level, they provide significant corroborating evidence to the osteological data.

In summary, the numerous (and in some cases major) differences in skull and tarsometatarsus morphology between *blewitti* and all other species of *Athene* (including *Speotyto*)—involving many cranial elements, especially the frontals, and the extremely stout tarsometatarsus—indicate that (although a rapid evolution cannot be excluded) *blewitti* seems likely to be distantly related to the others. Because of this distinctness, coupled with its unusual flight and tail-flicking behaviours, we consider the resurrection of the monotypic genus *Heteroglaux* fully justified, and far from 'spurious' (Weick 2006). Even those predisposed to recognise very broad genera, and who may thus prefer to maintain *blewitti* in *Athene*, should at least be aware that it is osteologically much the most distinctive of the group and quite possibly evolved from an ancient divergence event. Further study involving more owl taxa, such as phylogenetic analyses based on morphology and/or DNA, is likely to shed more light on the relationships of *blewitti*, but in the meantime we contend that the generic distinctiveness

of *blewitti* only increases the urgency with which the conservation needs of this Critically Endangered species must be addressed.

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